THE NATURE AND FORMATION OF SCALE INSECT SHELLS

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The armored scales (Coccidæ, Diaspinæ) are among the most interesting of all insects. They are the most specialized and anomalous of all known Homoptera. The remarkably degenerate structural condition of the females, which is correlated with, and in some way caused by, their sedentary habits, has resulted in an extraordinary sexual dimorphism, or pronounced structural difference between males and females (Fig. 1, *f* and *g*). Their great destructiveness to fruit and shade trees, ornamental shrubs, and florists' stock has also led to very extensive study of these insects.

Two questions of scientific and practical importance, however, appear not to be satisfactorily answered in the American literature dealing with the armored scale insects. *First,* what is the composition, or chemical and physical nature, of the shell or scale that covers the bodies of the insects; and *secondly,* how is the covering scale formed about the insect?

It has been well known that the secretion which forms the shell or case exudes from glands opening chiefly at the posterior end of the body (Fig. 4). We became interested in the question how a legless and presumably motionless insect can distribute a substance, formed at its tail end only, uniformly and symmetrically around the body in more or less concentric rings or crescents of increment as growth proceeds. It is also difficult to account for the actual mechanics of formation of a hard shell that completely covers the body of the insect making it, and yet allows for a steady and continuous growth. Does the wax, in a molten condition, flow out to the margins of the body; is it forced out by the weight of the shell already formed; or is it placed about the margin by some part of the insect's body? The American literature seems strangely silent on this point. None of the general texts nor the special bulletins on scale insects that we have consulted attempt to explain how the female insect places her secretions around the body. An American monographic work of 500 pages on the Coccidae contains

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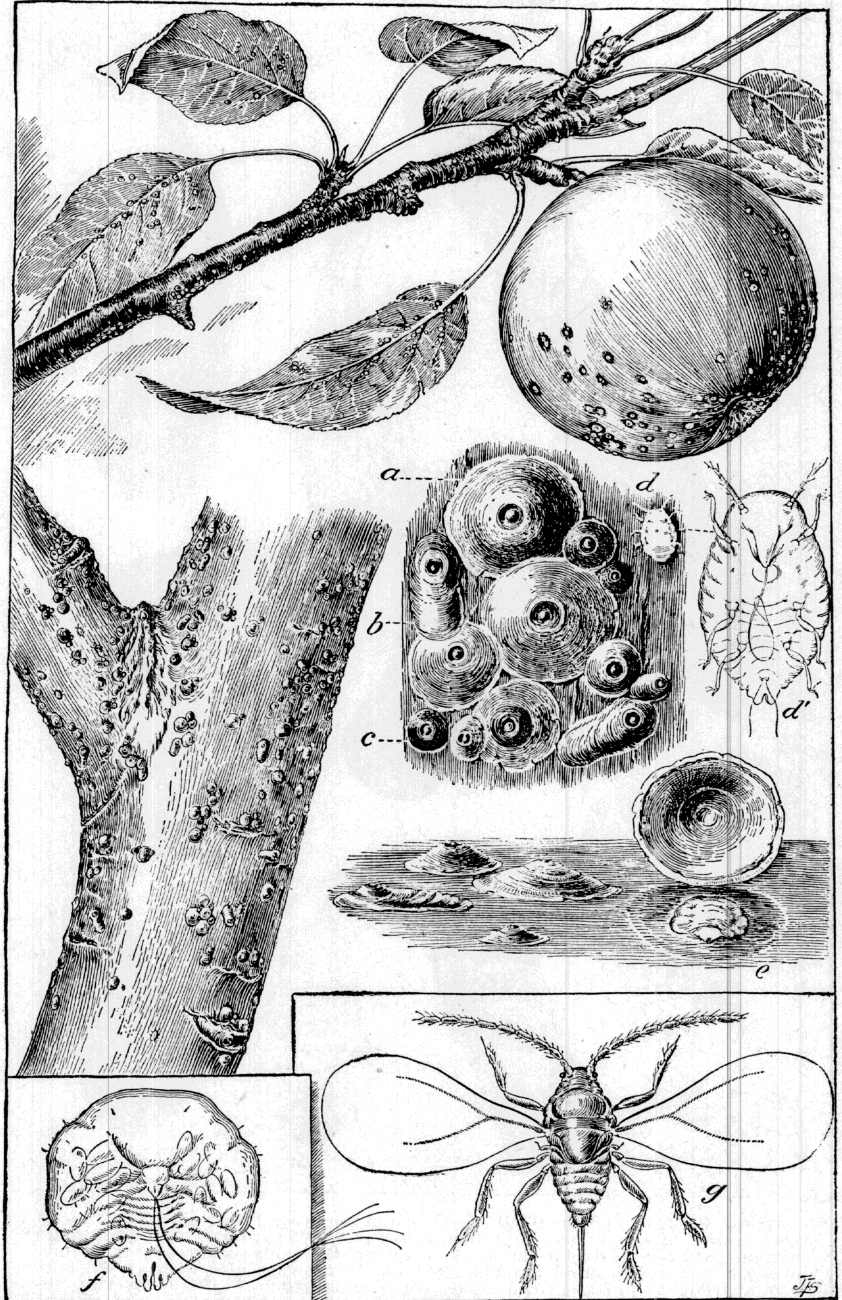

FIG. 1. The San José Scale: *a,* shell covering adult female; *b,* more elongate shell covering the developing male; *c,* shells covering young scales; *d,* first instar nymph or "crawler"; *d,* the same, much enlarged; *e,* shell lifted to show the body of the female beneath; *f,* body of the adult female, more enlarged; *g,* adult male. *(From U. S. D. A. Farm Bul. 650.)*

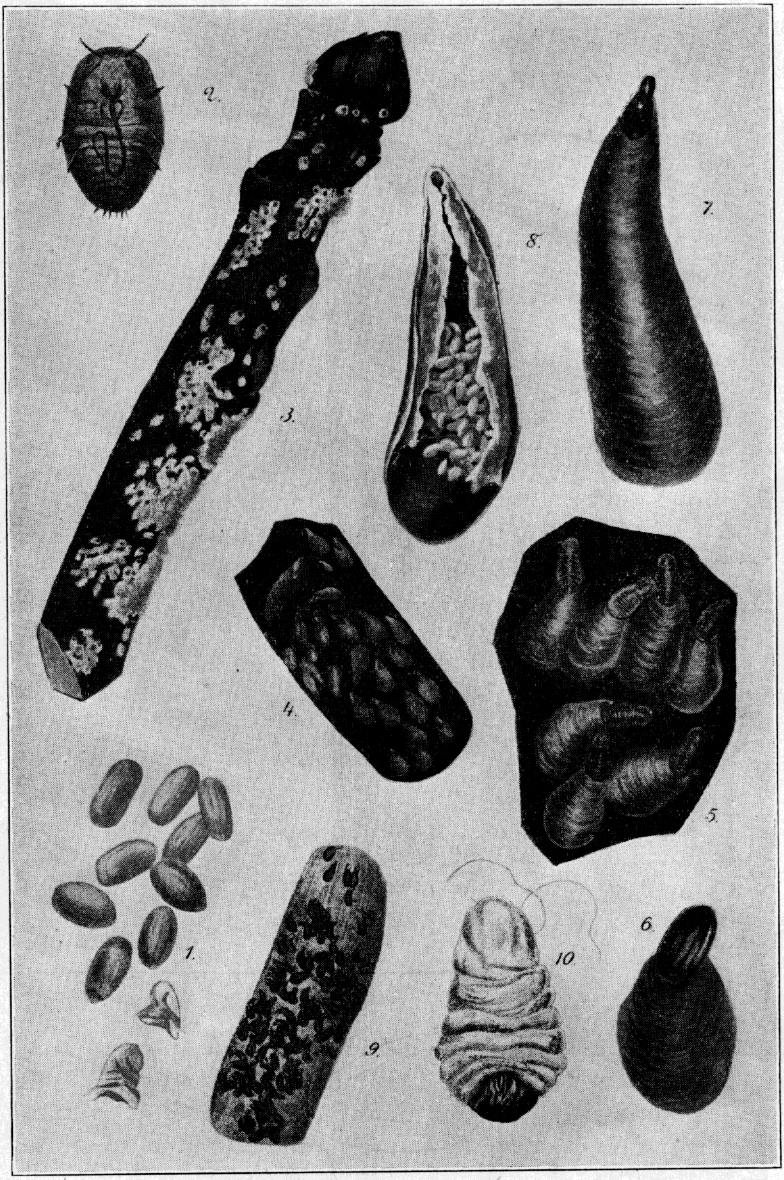

FIG. 2. The Oyster Shell Scale: (1) eggs and two shriveled shells, very much enlarged; (2) first instar nymph or "crawler"; (3) first instar nymphs after settling on the bark, showing the whitish threads that form over the back of the first nymphs; (4) partly grown scales with an old one; (5) a group of partly grown scales, more enlarged; (6) shell covering the developing male—note the single terminal exuvia, and the lines of growth on the shell; (7) shell covering the adult female—note the two exuviae at the anterior end and the lines of growth on the shell; (8) shell of female turned over, showing remnants of the ventral shell, the eggs filling most of

not a word on this point. Inquiry among a number of entomologists revealed to us a general lack of understanding of this point. We, therefore, present the following contribution toward a wider understanding of this interesting question.*

To anyone examining one of the armored scales, it is obvious that the shell is composed of two different parts. One part is clearly the shed skin, or exuvia, of the young insect. The other part is as clearly an amorphous plate or shell and, upon microscopic examination, the latter is seen to be knitted or spun from innumerable threads which are so closely interwoven, or packed together so tightly as to appear like little pellets held together by minute threads to form a firm membrane. (Fig. 8.)

There are two principal types of these shells or scales; one (Fig. 2, *6* and 7) in which the exuviae occupy a position at one end, with most of the shell developed in concentric bands toward the other end ("exuviæ terminal"); and another (Figs. 1 and 5) in which the shell is more or less uniformly distributed in concentric rings about the central exuviae. Various intermediate conditions are found in which the exuviae are more or less eccentric but not terminal.

Before proceeding to a discussion of the formation of these shells we may review briefly the events in the life-cycle of the insect which are necessary to an understanding of the nature of the scale or shell. Eggs are laid under the shell, as in the Oyster Shell Scale (Fig. 2, *1* and *8*); or the young are born as active crawling nymphs without any exposed egg stage. The minute nymphs (Fig. 2, *2;* and 1, *d* and *d'*), which are provided with six, well-developed legs, a pair of long antennæ, large simple eyes, and functional piercing-sucking mouth parts, are indistinguishable as to sex. They crawl about over the host plant for a few hours during which they may succeed in covering a few inches to a few feet distance.

Natural dispersal is entirely restricted to these minute nymphs or "crawlers." Their period of activity rarely exceeds a few hours and the distance covered is, ordinarily only a few feet. When an appealing spot on the host plant is found the nymph inserts its

* Since this article was submitted for publication, an article by Moriyuki Matsuda, "Studies on *Chrysomphalus aonidum* L. in Formosa," has appeared as Report No. 39 of the Dept. Agr. Gov't. Research Institute, Formosa, Japan, April, 1929, to which the reader is referred.

the shell and the dead shriveled body of the female at one end; (9) a group of female scales; (10) body of adult female removed from shell. *(From New York State Museum Bul., Vol. 9, No. 46, 1901.)*

mouthparts and, in the case of the female, the individual ordinarily never again moves from that spot. Since the flight of the adult male has no significance in dispersal, the natural spread of armored

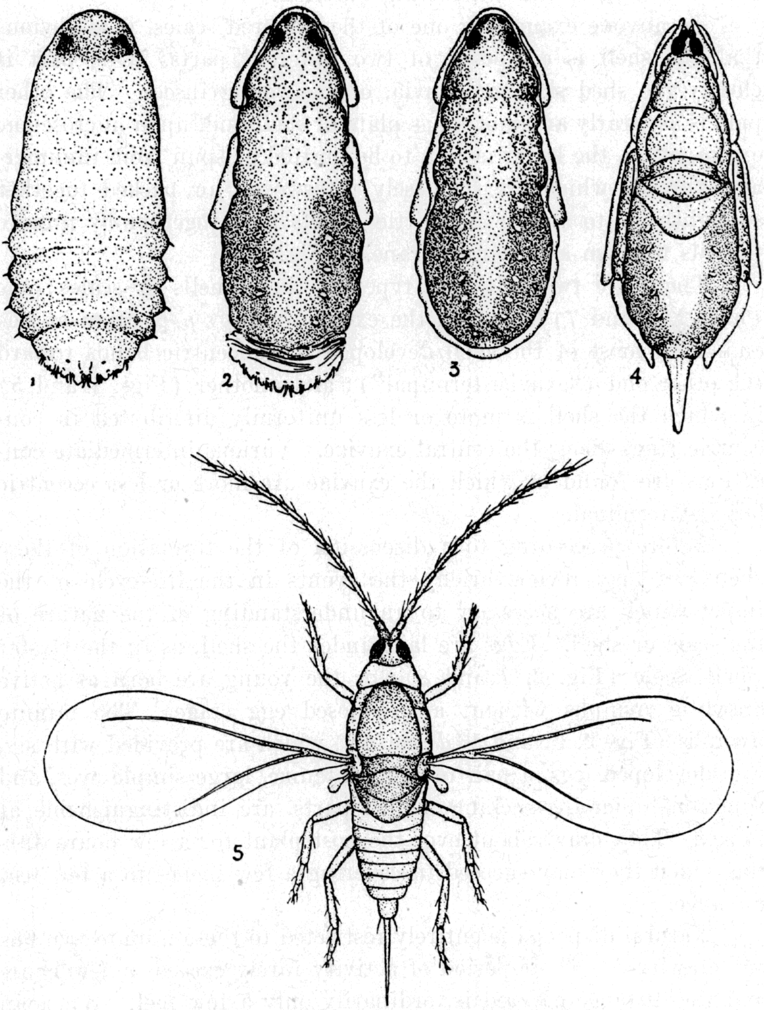

FIG. 3. The Purple Scale, *Lepidosaphes beckii* (Newman), showing the stages in metamorphosis of the male: (1) second stage nymph; (2) third stage nymph with exuvia of second stage adhering to tip of abdomen; (3) the same without exuvia; (4) fourth stage nymph; (5) adult male. All dorsal views and greatly enlarged. *(From Cal. Agr. Exp. Sta. Bul. 226.)*

scales is extremely restricted, and plants attacked become very heavily infested and frequently killed. The transportation of host plants has, however, carried some species to the ends of the earth.

As these first stage nymphs, which are mere specks in size, begin to feed, threads of a secretion from unicellular glands opening thru the skin appear over the back and soon completely cover it with a cottony mass (Fig. 2, *3*). These threads may break off and blow away. Sometimes, however, they mat down or fuse into a delicate, transparent membrane, or form a whitish knob or raised ring on top at the center of the scale. This is the uppermost and first part of the compound shell and some trace of it usually covers the exuviæ. Shortly after feeding begins, the first molt occurs, the insect splitting off its skin and slipping out on the under side leaving the dorsal part of its exuvia in place over its back to form the nucleus, nipple, or so-called exuvia of the scale.

At this first molt resemblance between males and females, which up to this time were indistinguishable, begins to disappear. The female loses her antennae, eyes and legs, nearly all trace of body regions and segmentation and becomes a mere bag of living substance with a sucking tube, formed by the mouthparts, at the middle of the under side of the body, as her only remaining appendage (Figs. 1, *f;* and 2, *10*). The female insect thus loses permanently nearly all of the characteristics of the class Insecta to which she belongs.

The metamorphosis of the female is a very simple one. The egg produces the active, six-legged, first instar nymph. The first molt transforms her to a sessile, legless, second instar nymph, like the adult except smaller in size, in being devoid of a genital orifice, and in lacking circumgenital glands. A second and final molt discloses the adult female (Figs. 1, *f;* and 2, *10*).

The males undergo a much more pronounced metamorphosis. At the first molt, which terminates the active, crawling, first nymphal stage and initiates the second instar, the male appears (Fig. 3, *1*) without legs, antennae and eyes, and is in a general way similar to his sisters although the body and the shell that covers it, is usually somewhat more elongate. After a few days the males molt again and in this third instar (Fig. 3, *2* and *3*) have lost all resemblance to the females. The mouth parts have entirely disappeared and the males never feed after this stage. They are somewhat pupa-like: the developing legs and antennæ, which arise from histoblasts, show externally, each enclosed in a separate case. They molt again, the legs and antennæ becoming larger, and the wing pads appear (Fig. 3, *4*). A conical projection at the tip of the abdomen contains the genital apparatus.

After a fourth and final molt the two wings expand beneath the shell and, according to Green (*l.c.*), the males crawl out backward, drawing the delicate wings up over and in front of the head. It is interesting to note that the wing pads are borne externally, thus properly placing the Coccidæ, along with other Homoptera, as exopterygota.

A comparison of adult males and females reveals the following extensive dimorphism:

Adult Male (Figs. 1 *g*; 3, *5*)	Adult Female (Figs. 1 *f*; 2, *10*)
Body insect-like with body regions evident.	Body gall-like, sack-like or scale-like with body regions indistinguishable.
A pair of large front wings. Hind wing rudimentary, usually consisting of a hook which engages a small pocket near the base of the front wing.	No trace of wings.
Three pairs of well-developed legs.	No trace of legs.
A pair of very rudimentary compound eyes and two pairs of ocelli or simple eyes, one on the dorsal and one on the ventral side of the head.	No trace of eyes.
Antennæ large and well-developed.	No trace of antennæ.
No mouth parts; takes no food. The male thus lacks the only appendage that the female possesses.	Mouth parts well-developed, often several times as long as the body. They consist of four stylets (the two mandibles and two maxillæ) which form a piercing organ and a sucking tube. When not inserted into the plant, the stylets lie in a delicate-walled invagination of the head forming a pouch into which they coil or loop before entering the plant tissues and in which all the slack of the stylets is held. The labium is greatly reduced and forms a tiny triangle at the base of the stylets.
Only one exuvia incorporated in the shell which is usually more elongate or more slender than that of the female (Fig. 1, *b*; 2, *6*).	Two exuviæ incorporated in the shell (Fig. 1, *a*; 2, 7.

The male has a prominent genital spike or sheath, which is slender and pointed and may be half as long as the body. It consists of a single piece with the margins rolled ventrally to form

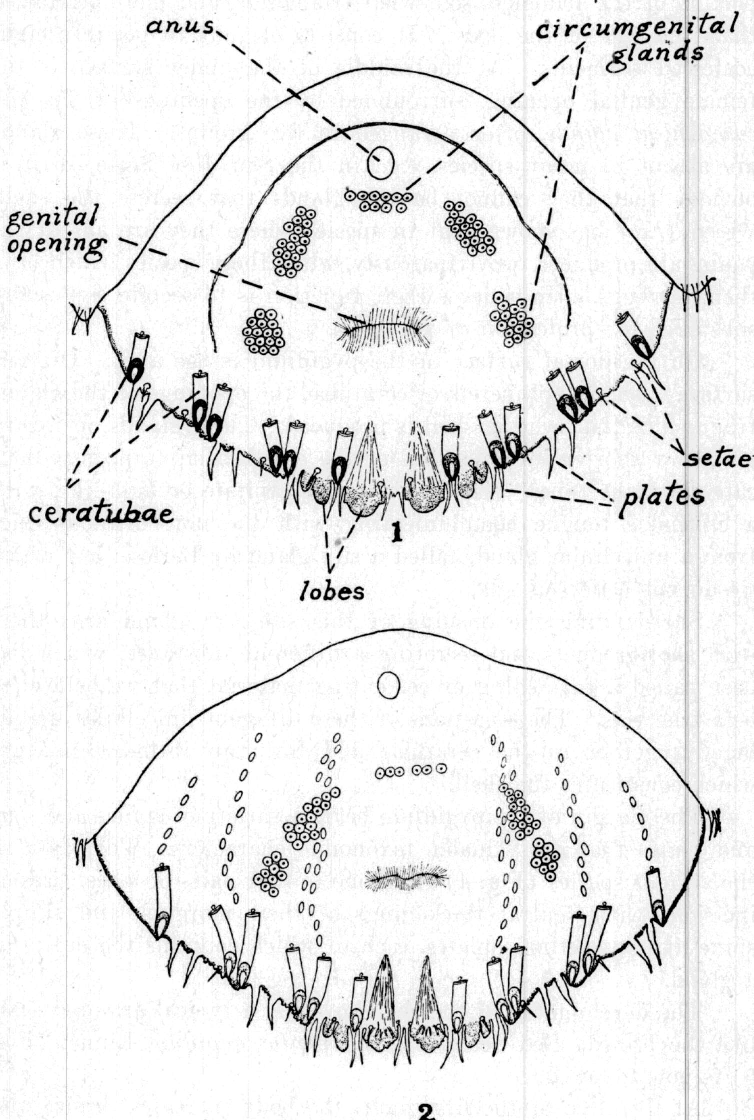

FIG. 4. The pygidia of two closely related scale insects: the Oyster Shell Scale, *Lepidosaphes ulmi* L., *above*; and the Purple Scale, *Lepidosaphes beckii* Newman, *below*. The genital opening and circumgenital glands show through from the ventral side. The secretion which forms the shell is poured out through the ceratubæ. *(From Miss. Agr. Exp. Sta. Tech. Bul. 2.)*

an incomplete tube through which the very elongate flexible penis is exserted to fertilize the female beneath her shell.

The pygidium of the female (Fig. 4) is a flattened, terminal portion of the abdomen, somewhat triangular, and more chitinized than the rest of the body. It consists of four to possibly eight coalesced segments. At the middle of the under surface is the female genital opening, surrounded by the openings of the *circumgenital glands,* often arranged in five groups. These glands are absent in many species, e.g., in the San José Scale, so it is obvious that they cannot be the glands that secrete the shell. Green (*l.c.*) has shown that in species where they are absent the young are produced ovoviviparously, while those species which have them lay eggs. He believes their function is to secrete a powdery substance for protection of the eggs.

On the dorsal surface of the pygidium is the anus. On this surface open the spinnerets or ceratubæ, the openings of the glands from which the covering shell is produced. These glands open thru longer or shorter invaginations of the cuticle that form very delicate chitinous tubes. The inner end is capitate or bulb-like, with a chitinous tongue communicating with the non-chitinous duct from a unicellular gland, called a silk gland by Berlese, but which we do not believe is silk.

Surrounding the opening of this silk (?) gland are others with shorter ducts and secreting a different substance, which has been called a varnishing or cementing material that we believe to be a true wax. The secretions of these different unicellular glands blend together in the ceratubæ and form an intimate mixture which constitutes the shell.

The margin of the pygidium bears a variety of spines and setæ and plates that are valuable taxonomic characters. There are in the various species (Fig. 4) from one to four pairs of lobes, various incisions with ventral thickenings of their margins, and simple spine-like or pectinate plates, each of which contains the outlet of a gland.

The development of the shell covering a typical armored scale like the Florida Red Scale, *Chrysomphalus aonidum* Linné, (Fig. 5) is now followed.

At the time of the first molt, the body increases in size and to cover it an extension is made all around the shed skin or exuvia, consisting of closely woven filaments, so packed together as to form a very firm but thin shell or membrane.

This second addition to the shell is in the form of a disc with a hole at its center, since the secretion does not extend over the middle region or back of the second instar nymph. The first exuvia is more or less covered above with the secretion formed during the first nymphal instar; its margins fit into the disc formed

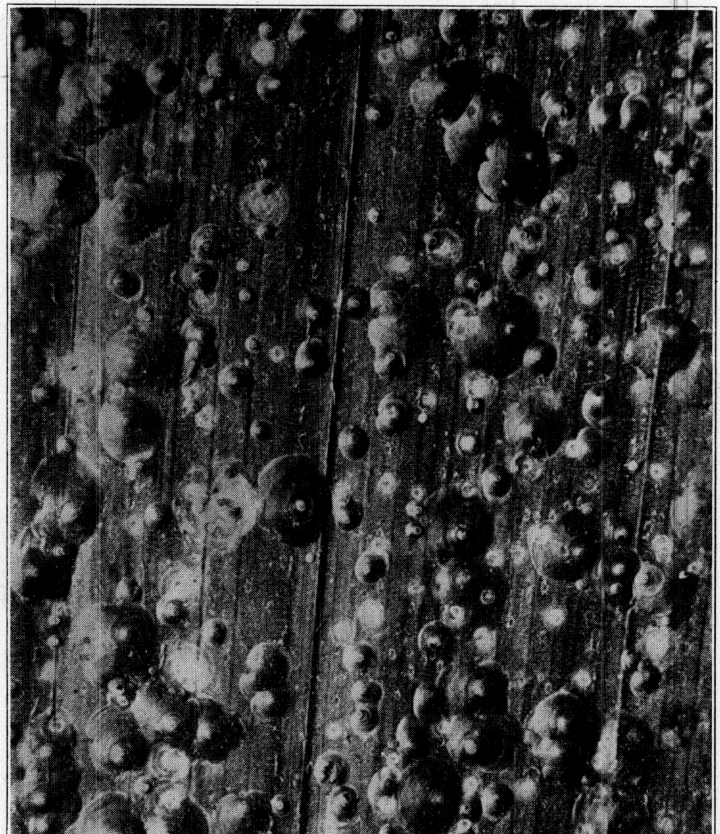

FIG. 5. The Florida Red Scale, *Chrysomphalus aonidum* L., showing scales of adults and nymphs of various sizes on palm leaf. Note the central exuviæ and the indications of successive rings of growth on the larger scales. *(From Mich. Agr. Exp. Sta.)*

by the second nymph much as a crystal fits in the face of a watch; but it is exposed on the under side except for a little secretion which formed a very thin ventral scale for the first instar nymph.

After a period of feeding and growth during which the shell or covering scale keeps pace with the increase in size of the body, a second and last molt takes place, the insect slipping out beneath as before and assuming its final form called the adult. This is very similar to the second stage nymph, except that it is much larger.

The second shed skin, like the first, becomes incorporated in the scale, being cemented to the upper and earlier part by its margins only and by the very thin ventral scale of the first instar nymph. At this stage copulation with the winged male occurs. The

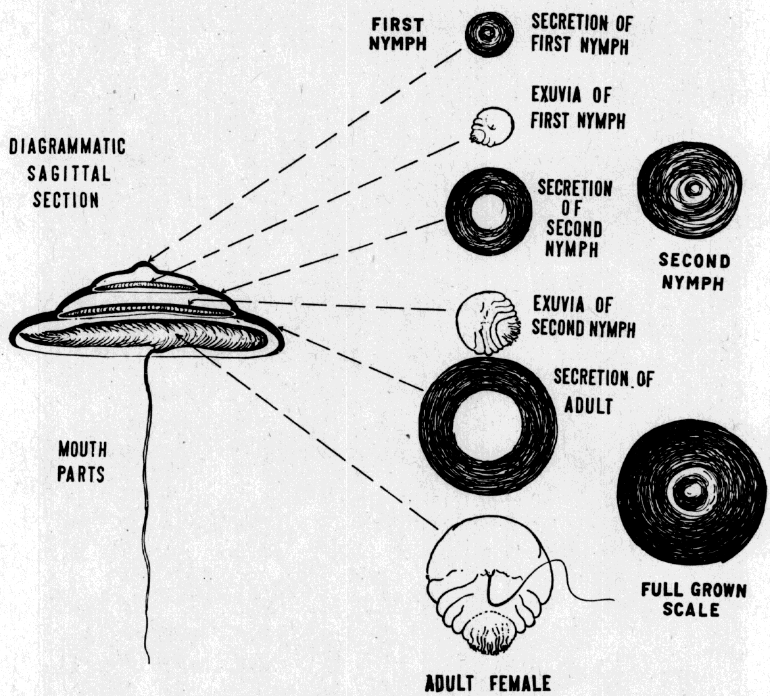

FIG. 6. Diagram to show the structure and development of an armored scale. *(Original.)*

fecundated female expands in size, outgrowing her covering, and another and final addition is made to the house. This is added as a concentric ring or band around the margin of the second exuvia, and not extending across the middle region.

The scale is thus seen to consist of five distinct parts or increments (Fig. 6): (1) the secretion over the back of the first instar nymph, which is sometimes largely worn away; (2) the shed skin of the first nymph; (3) the flattened ring of secretion made by the second instar nymph; (4) the shed skin of the second instar nymph; and (5) the flattened ring of secretion made by the adult female. Finally, beneath all this, is the living body of the female.

When the complex composition of the scale was discovered, the problem of how it was formed became all the more puzzling. As stated above, all the American literature known to us is strangely silent on this point.

It became evident to the authors that the only theory that could account for the symmetrical distribution of the secretion, from glands opening only at the anal end of the body, is that the legless female must rotate her body completely around in a circle beneath her shell, painting the semi-fluid secretion in concentric rings as she goes. After having formulated this theory, we discovered in Green's monographic work (*l.c.*) the following statement:

> "In some genera, such as *Aspidiotus* and *Diaspis* ....the insect must revolve completely around the point of attachment during the construction of the puparium. In the genera forming elongate puparia, a to-and-fro sweeping motion of the hinder parts of the body is sufficient to produce the resulting form of scale."

Berlese in *Le Coccíniglie Italiane* says (translation):

> "The larvæ of *Aspidiotus* and *Aonidiella* form the first layer of silk, perfectly circular, and may get this shape by turning around, while spinning, upon the center of their bodies as an axis.
>
> "In *Aspidiotus* and *Aonidiella* all the species spin by turning around upon themselves; therefore the dorsal scale and the leaf-like ventral scale are composed of threads which combine into so many concentric circles and are discoidal in form.
>
> "In *Mytilaspis* and *Parlatoria zizyphi,* however, the insect spins while swinging the body in a light oscillating motion from right to left, from which the threads form as many crescents in a row and the whole shield is drawn out in length rather than being round."

Contrary to the supposition of many people, the female, altho legless and sedentary, is not motionless. Proof that this theory is correct was found by soaking the scales in potash solution when they could be separated by careful dissection into their component parts. Since the pygidium is recognizable in each of the molted skins and the posterior end of the body thus definitely marked, it is obvious that if the three do not all point to the same point of the compass, the body of the insect has rotated.

Examination of a number of scales gave the following results. As the shell was lifted, the position of the adult pygidium was marked with a notch in the margin of the shell. After soaking in potash the corresponding posterior end or pygidium in the first and second exuviæ could be seen. Taking the position of the adult pygidium as 12 o'clock in each case, those of the nymphs in five unselected cases stood as follows:

Adult	12	12	12	12	12
2nd Nymph	6	11	3	10	9
1st Nymph	2	8	1	7	4

How the body moves, whether clockwise or counter-clockwise, or how many times it completes the circuit we do not yet know. The examination of the shells of certain species shows some evidence of successive rings arranged in a spiral (Fig. 5), which indicate that the adult insect rotates at least several times during her life. The complex lobes, spines, and the plates of the pygidium (Fig. 4) may be used as prys or prickers to gain leverage against leaf or bark and enable the insect to push her muscular body sidewise, while it is anchored at the center by the mouth parts. They serve as bristles of a paint brush, the pectinate and spine-like plates having wax glands opening in their margins. Is it possible that their complex nature is in part correlated with the nature of the leaf or bark surface over which their lubberly bodies must shift?

In the case of a scale with exuviæ terminal (Fig. 2, 6 and 7) it is obvious that the tip of the body is simply lashed from side to side as the secretion exudes and the increments are painted on in successive crescents.

The other question as to the composition or chemical and physical nature of the secretion which forms the major part of the scale, is quite as unsatisfactorily answered in the literature. Nearly all the literature we have consulted refers to the scale of the Coccidæ as a wax or waxy secretion. Berlese speaks of it as spun silk excreted from the rectum. Green calls it "waxy, fibrous or resinous matter." It was probably the general opinion regarding its waxy nature that led Maulick a few years ago to attempt the solution of the scale in wax-solvents in the hope of improving the known insecticides for scale insect pests. He immersed twigs of elm, bearing Oyster Shell Scale (*Lepidosophes ulmi* Linné) in each of 17 different known wax solvents for nearly a year. At the end of this time he reports that no action seemed to have taken place and he concluded that the scale is most probably not a wax.

In our investigations the Oyster Shell Scale (*Lepidosaphes ulmi* Linné) was gathered by scraping from common Lilac (*Syringa vulgaris*) and extracted in a Soxhlet extractor. Ether extracted only 11% of the total weight of the dried scales and, since the eggs and dead bodies would furnish considerable fatty matter, it was evident that but little wax had been taken from the scales themselves. Carbon tetrachloride extracted an additional 24% of the original weight of the scales, making a total of 35% of the weight of the scales which yielded to wax solvents. Since a considerable portion of this might have come from the dead females and eggs remaining as a contamination of our material, we next undertook the tedious task of scraping out eggs and dead bodies of females from a quantity of these shells, leaving only the clean shells and their exuviæ.

These yielded to extraction with hot carbon tetrachloride 58% of their original weight. Next some of the scales were taken and the exuviæ cut off, leaving nothing but the pure secretion of the female insects. This gave, with hot carbon tetrachloride, 71.8% wax dissolved out. This shows that there is less wax, if any at all, in the exuviæ.

After extraction of the wax with carbon tetrachloride the scales looked somewhat lighter in color and were slightly shrunken in size but the fact that no great difference in appearance results is shown by the picture (Fig. 7) of the twigs bearing scales, two of which were extracted by carbon tetrachloride until no more wax could be removed, the others untreated. Microsections of the extracted scale (Fig. 9) showed the insoluble part to be homogeneous in structure and tending to split into layers which however show no signs of uniformity and are doubtless irregular planes of weakness in the scale. It is now quite clear why Maulick recognized no change in the scales which he treated with wax solvents for a year. Even though a considerable quantity of wax had been extracted the gross appearance of the scale would not have been appreciably altered. It is only when one compares a micro-section of an extracted with an unextracted scale that one sees where the wax has come from. The relation between the cross-section of the extracted and unextracted scales is shown in figures 8 and 9.

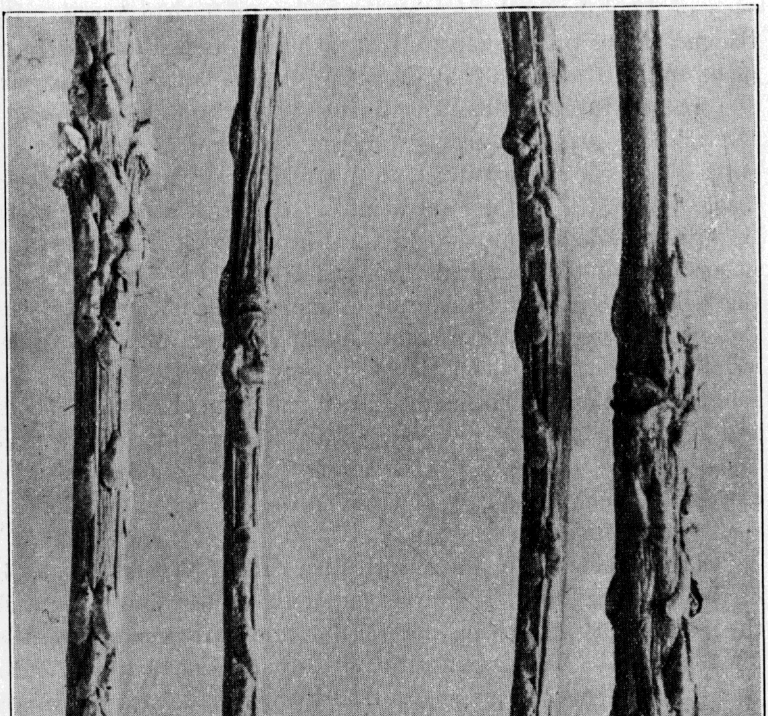

FIG. 7. Twigs of Lilac bearing Oyster Shell Scales. The two twigs on the left have been treated with hot carbon tetrachloride until one-third of the weight of the scales has been extracted; the other two twigs have not been treated. Note that the loss of one-third the original weight of the shells has scarcely altered their gross appearance. *(Original.)*

The part of the scale left after extraction with carbon tetrachloride was tested for chitin by the method suggested by Campbell (1929) and gave negative results. The extracted scales became colorless and then dissolved in the concentrated potassium-hydroxide solution used in this method. It was thought possible that the scales might merely have disintegrated into a colloidal

FIG. 8. Two microsections of an Oyster Shell Scale, which had not been treated with wax solvents. Compare Figure 9. *(Original.)*

state; but when the alkali was neutralized with acid and the solution evaporated to dryness the only material left that gave a test for chitin was the exuviæ, which had not dissolved or disintegrated. Scales, which had been extracted with carbon tetrachloride but not boiled in alkali, gave negative tests for protein, using Millon's reagent and the xanthoproteic test. Attempts to hydrolize the scales and recover amino acids also failed; but a sodium fusion test showed the presence of nitrogen. The exact chemical nature of the non-waxy part of the scale is thus left in doubt.

FIG. 9. Microsections of Oyster Shell Scales after treatment with hot carbon tetrachloride to extract the wax. Note the splitting of the shell into layers. Compare Figure 8. *(Original.)*

A similar extraction was carried out on the Florida Red Scale (*Chrysomphalus anonidum* Linné) as collected from two different host plants, namely Kentia and Dracenæ. The wax totalled 31% and 34% respectively, in the case of the scales collected from

Kentia and Dracenæ. Since this difference is within the range of probable error it indicates that the nature of the shell is specific for the insect and unaffected by the host plant. The Pine Leaf Scale (*Chionaspis pinifolia* Fitch) gave 40.3% extracted wax with carbon tetrachloride while the Fluted Scale (*Icerya purchasi* Mask.) gave 98% or more of wax, being nearly pure. Some extractions of the exuviæ alone showed that little or no wax was contained in this part of the scales. It was further found that the scale once extracted could not be made to reabsorb any of the wax.

The solubility at room temperature of the Oyster Shell Scale wax in grams per c. c. was found to be:

With ethyl acetate	.0059
With ether	.0084
With carbon tetrachloride	.0008
With carbon disulfide	.0041
With ethyl alcohol	.0005

The waxes were readily soluble in carbon tetrachloride only at high temperatures near the boiling point, ether being a better solvent *at room temperature* than carbon tetrachloride.

The wax was found to be a mixture in all cases and to be specific for each insect even though they had fed on widely different hosts. The wax from the Oyster Shell Scale melts at 94-96° C. and this lack of a sharp melting point shows it is not a pure compound, but a mixture of several waxes. The Florida Red Scale wax melts at 88-90° C., and the Fluted Scale wax fairly sharply at 80.50° C., and the Pine Leaf Scale at 86-88° C. The wax of the Fluted Scale thus differs from the others in that it seems to be nearly pure and is probably chiefly ceryl cerotate, which is known to be the chief constituent of "china wax," the commercial extract of a species of *Coccus*. Pure ceryl cerotate melts at 82.5° C. and pure china wax at 80-81° C. Some of the Oyster Shell Scale wax was partially purified by fractional crystallization and found to melt then at 98-99° C. There is only one known wax that melts at so high a temperature and this is cocceryl coccerate melting at 106° C. Hence, it seems highly probable that the wax of Oyster Shell Scale is largely cocceryl coccerate mixed with some other wax, probably of lower melting point.

CONCLUSIONS

The legless female insect underneath her skin is not motionless although she is quite sedentary. In the case of circular scales her body rotates thru a complete circle at least once in each life-stage, as the secretion from her anal glands is distributed in concentric rings. In the case of elongated scales with terminal exuviæ the tip of the abdomen is lashed from side to side to distribute the secretion in successive arcs of larger and larger radius.

The scale of the female Florida Red Scale, which shows superficially as two parts, proves upon analysis to consist of 5 distinct increments: (a) A thin central disc lying above the first exuvia and secreted by the first instar nymph; (b) the exuvia of the first instar nymph; (c) the flattened ring of secretion made by the second instar nymph; (d) the exuvia of the second instar nymph; (e) the flattened ring of secretion made by the adult female.

The secretion which forms the hard covering of armored scale insects is an intimate mixture of a wax with some other material. The wax is specific for each species of scale, and varying in the cases tested from 30% in the Circular Scale, 35% in the Oyster Shell, and 40% in the Pine Leaf Scale, to 98% in the Fluted Scale. The remaining 65% of the shell of the Oyster Shell Scale is apparently not chitin according to Campbell's method, and the usual tests do not indicate silk or proteins, although nitrogen is certainly present.

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